

THE MARINE ENCHYTRAEIDAE (ANNELIDA, OLIGOCHAETA) OF
THE EASTERN COAST OF NORTH AMERICA WITH NOTES ON
THEIR GEOGRAPHICAL DISTRIBUTION AND HABITAT ¹

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The Enchytraeidae, a reputedly difficult family of Annelida Oligochaeta from a taxonomic standpoint, include marine representatives. Many genera and species are wide spread in their distribution.

In spite of the fact that many species occur in great abundance along the Atlantic coast of North America, they have received scant attention from workers. Only eight papers dealing with marine Enchytraeidae have appeared in North America. From the Atlantic coast, Minor (1863) gave a description of *Enchytracrus triventralopectinatus*, found near the high-water mark at New Haven, Connecticut. This species seems to be the naidid *Paranais litoralis* Müller, as supposed by Michaelsen (1900). Verrill (1873) described *Halodrilus littoralis* but its synonymy with *Enchytracrus albidus* Henle was later established by Michaelsen (1900); Verrill (1873, page 623) reported it from New Haven, Woods Hole and Casco Bay, Maine, as "very common under dead sea-weeds and stones near high-water mark." Smith (1895) made an anatomical study of this oligochaete at Woods Hole, using the name of *Enchytracrus littoralis* Verrill. Moore (1905) reported two species, *Enchytracrus albidus* and *Lumbricillus agilis*, probably a synonym of *Lumbricillus lineatus* (Müller), to be very abundant at Woods Hole, Vineyard Sound, Massachusetts, as well as along the coast from Casco Bay, Maine, to Sea Isle City, New Jersey. Welch (1917) carried out some ecological observations and experiments in methods of culture with *Enchytracrus albidus* and *Lumbricillus lineatus* at Woods Hole. Recently Kennedy (1966) described a new species referred to the genus *Grania* Southern 1913, from marine localities off the coast of Bimini and Panama City, Florida.

Eisen (1904), a pioneer in enchytraeid taxonomy, described eleven new marine species which are apparently limited to the Pacific west coast of North America. The descriptions were based principally on Enchytraeidae collected by the Harriman expedition to Alaska in 1899. The general procedure observed in modern descriptions of Enchytraeidae, renders indeterminable many species described before 1930. Eisen's species need critical revision; however, with type series for comparison, most of them, carefully described, would probably survive. More recently Altman (1931) described *Enchytracrus pugetensis* from Puget Sound, Washington; this species was included in the genus *Marionina* Michaelsen by

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Nielsen and Christensen (1959); due to the poor quality of the description this species is indeterminable.

During the spring 1969, the author carried out some studies on the systematics and ecology of marine Enchytraeidae living in Massachusetts and North Carolina, limited largely to salt marshes and intertidal areas in the vicinities of Woods Hole and Beaufort. Material from a survey of the fauna of Cape Cod Bay, Massachusetts, which is conducted by the Biotic Census of the Systematics-Ecology Program, Marine Biological Laboratory, was found to contain three abundant species, two of these new to science. The ecological interest of the study was suggested by the unique locations of Massachusetts and North Carolina, since the environs of Woods Hole and Cape Cod Bay have a cold environment in the boreal biogeographic province, in contrast to the Carolinian province which displays boreal and temperate features. The principal results suggest interesting problems of distribution and tolerance.

METHODS

Marine Enchytraeidae were identified from 200 samples collected by the author, in the spring of 1969 at 20 stations in the environs of Woods Hole, Massachusetts and Beaufort, North Carolina. One part of each sample was preserved in a solution of 10% formalin in seawater. The living animals in the non-preserved samples were extracted qualitatively by simple washing and filtering on nylon screens of 0.1 mm to 0.5 mm mesh diameter. The formalin-preserved animals were quantitatively extracted by washing the whole sample through a series of screens down to 0.5 mm mesh diameter. The formalin-preserved animals were separated from the residue under slight magnification, briefly immersed in a solution of 10% formalin in seawater and stored in 85% ethyl alcohol (Lasserre, 1967a, Hulings and Gray, 1971). Nineteen quantitative samples from Cape Cod Bay, Massachusetts contained enchytraeids. The samples were taken with a 0.1 m² Smith-McIntyre grab. Material was washed through a series of screens down to 0.5 mm mesh diameter, narcotized in a solution of 0.015% propylene phenoxetyl, fixed for 48 hours in a solution of 10% formalin in seawater, then stored in 85% ethyl alcohol.

As a general rule only mature enchytraeids were examined. Their anatomy was observed by one, or a combination of three methods: (a) living worms were placed on a slide with a drop of water and covered with a cover-slip; the size and weight of the cover slip and the amount of water barely allow the worm restricted movements; (b) the fixed worm was lightly stained in Borax carmine of Ehrlich's acetic haematoxylin (Pantin, 1962) and mounted whole in Canada balsam; (c) the genital regions were sectioned at 5 μ and stained in Heidenhain's haematoxylin and eosin (Pantin, 1962).

The sediment was analyzed for particle size through a nest of U. S. Standard Sieves, each separated by one phi-unit. The sieves used had mesh openings of 4.000 mm, 2.000 mm, 1.000 mm, 0.500 mm, 0.250 mm, 0.063 mm. In the environmental data "Gravel" refers to particles larger than 2.000 mm, and "silt-clay" to particles smaller than 0.063 mm; "So" is the sorting coefficient, $So = \sqrt{Q1/Q3}$ (Trask, 1932), where Q1 and Q3 are, respectively, the first and the third quartiles, plotted on the cumulative curves. A well-sorted sediment has a sorting index

ranging from 2.30 to 1.40; a very well-sorted sediment has a sorting index ranging from 1.40 to 0.50.

Environmental data for the principal stations are given below.

Massachusetts

Station 1: 41°32.30'N, 70°38.10'W; Falmouth Harbor beach. Salt marsh, mean particle size 0.400 mm, $So = 1.29$. Gravel 35.40%, sand 64.38%, silt-clay 0.22%.

Station 2: 41°31.00'N, 74°40.00'W; Nobska Beach, Woods Hole. Intertidal, semi-protected, high tide mark, depth in substratum 0.20 m; mean particle size 0.900 mm, $So = 1.63$. Gravel 19.20%, sand 80.78%, silt-clay 0.02%.

Station 3: 41°32.00'N, 70°40.00'W; Gansett Beach, Woods Hole. Intertidal, semi-protected, high tide mark, depth in substratum 0.10 m; mean particle size 0.500 mm, $So = 1.46$. Gravel 35.22%, sand 64.71%, silt-clay 0.07%.

Station 4: 41°35.00'N, 70°39.00'W; Wood Neck Beach; Sippowisset. Intertidal, semi-protected, mean high tide mark, depth in substratum 0.20 m; mean particle size 0.400 mm, $So = 1.69$. Gravel 15.00%, sand 84.80%, silt-clay 0.20%.

Station 5: 41°31.41'N, 70°40.41'W; Crane's Beach, Woods Hole. Intertidal, semi-protected, mean high tide mark, depth in substratum 0.10 m; mean particle size 0.500 mm, $So = 1.18$. Gravel 35.71%, sand 64.28%, silt-clay 0.01%.

Station 6: 41°32.00'N, 70°41.00'W; M. B. L. Beach, Woods Hole. Intertidal, semi-protected, mean high tide mark, depth in substratum 0.10 m; mean particle size 0.720 mm, $So = 1.40$. Gravel 33.20%, sand 66.70%, silt-clay 0.10%.

Stations of the Systematics-Ecology Program's Biotic Census, in Cape Cod Bay

0612-E1: 42°02.30'N, 70°08.00'W; depth 10.98 m; mean particle size 0.880 mm, $So = 0.39$. Gravel 2.10%, sand 96.20%, silt-clay 1.70%.

1412-E1: 41°54.30'N, 70°08.00'W, depth 15.55 m; mean particle size 1.490 mm, $So = 0.54$. Gravel 28.03%, sand 71.51%, silt-clay 0.45%.

1412-E4: 41°54.00'N, 70°08.40'W; depth 17.08 m; mean particle size 0.795 mm, $So = 0.52$. Gravel 2.69%, sand 97.27%, silt-clay 0.01%.

1530-E3: 41°53.00'N, 70°31.20'W; depth 12.20 m; mean particle size 0.336 mm, $So = 0.68$. Gravel 0%, sand 99.98%, silt-clay 0.01%.

1730-E3: 41°51.00'N, 70°31.20'W; depth 8.54 m; mean particle size 0.576 mm, $So = 0.64$. Gravel 0%, sand 99.99%, silt-clay 0%.

1812-E1: 41°50.30'N, 70°08.00'W; depth 2.74 m; mean particle size 0.552 mm, $So = 0.61$. Gravel 0%, sand 98.99%, silt-clay 0.99%.

1812-E2: 41°51.00'N, 70°07.10'W; depth 2.13 m; mean particle size 0.702 mm, $So = 0.50$. Gravel 2.28%, sand 97.71%, silt-clay 0%.

1812-E4: 41°50.00'N, 70°08.50'W; depth 4.27 m; mean particle size 0.402 mm, $So = 0.66$. Gravel 0.06%, sand 99.92%, silt-clay 0%.

1812-E5: 41°51.00'N, 70°08.50'W; depth 3.05 m; mean particle size 0.461 mm, $So = 0.64$. Gravel 0%, sand 99.98%, silt-clay 0%.

1910-E1: 41°49.30'N, 70°05.30'W; depth 6.71 m; mean particle size 1.021 mm, $So = 0.41$. Gravel 24.32%, sand 74.84%, silt-clay 0.82%.

- 1910-E2: 41°50.00'N, 70°04.40'W; depth 6.71 m; mean particle size 0.868 mm.
So = 0.51. Gravel 4.48%, sand 95.48%, silt-clay 0.01%.
- 1930-E2: 41°50.00'N, 70°31.20'W; depth 10.37 m; mean particle size 0.694 mm.
So = 0.65. Gravel 0.16%, sand 99.82%, silt-clay 0%.
- 1930-E3: 41°49.00'N, 70°31.20'W; depth 11.89 m; mean particle size 0.698 mm.
So = 0.64. Gravel 0.44%, sand 99.54%, silt-clay 0%.
- 2008-E5: 41°49.00'N, 70°03.15'W.
- 2028-E5: 41°49.00'N, 70°30.00'W; depth 18.80 m.
- 2130-E2: 41°48.00'N, 70°31.20'W; depth 6.71 m, mean particle size 0.466 mm.
So = 0.58. Gravel 0.06%, sand 98.86%, silt-clay 1.07%.
- 2318-E1: 41°45.30'N, 70°16.00'W; depth 14.64 m, mean particle size 0.740 mm.
So = 0.52. Gravel 5.51%, sand 93.39%, silt-clay 1.07%.
- 2318-E4: 41°45.00'N, 70°16.40'W; depth 14.94 m, mean particle size 0.674 mm.
So = 0.23. Gravel 36.25%, sand 61.83%, silt-clay 1.86%.

North Carolina

- Station 1: 34°44.40'N, 76°39.40'W; Newport River, North Gallant Point. Salt marsh; mean particle size 0.300 mm, So = 1.79. Gravel 0%, sand 99.98%, silt-clay 0.02%.
- Station 2: 34°45.40'N, 76°44.10'W; Newport River, Lawton Point. Salt marsh; mean particle size 0.350 mm, So = 1.29. Gravel 0%, sand 99.97%, silt-clay 0.03%.
- Station 3: 34°43.30'N, 76°55.30'W; west of Morehead City. Intertidal, semi-protected, mean high tide mark, depth in substratum 0.20 m; mean particle size 0.440 mm, So = 1.59. Gravel 0%, sand 99.98%, silt-clay 0.02%.
- Station 4: 34°42.43'N, 76°40.55'W; Radio Island, Beaufort. Intertidal, semi-protected, mean high tide mark, depth in substratum 0.20 m; mean particle size 0.350 mm, So = 1.80. Gravel 1.00%, sand 98.64%, silt-clay 0.36%.
- Station 5: 34°41.55'N, 76°35.00'W; west of Harkers Island. Intertidal, semi-protected, mean high tide mark, depth in substratum 0.20 m; mean particle size 0.360 mm, So = 1.30. Gravel 0%, sand 99.98%, silt-clay 0.02%.
- Station 6: 34°41.10'N, 76°31.45'W; Harkers Island, Shell Point. Intertidal, exposed, mean high tide mark, depth in substratum 0.30 m; mean particle size 0.400 mm, So = 1.73. Gravel 0%, sand 99.95%, silt-clay 0.06%.
- Station 7: 34°40.50'N, 76°55.34'W; Bogue Banks. Intertidal, exposed strand, mean high water mark, depth in substratum 0.30 m; mean particle size 0.350 mm, So = 1.14. Gravel 0%, sand 99.98%, silt-clay 0.02%.
- Station 8: 34°41.50'N, 76°44.04'W; Bogue Banks, Atlantic Beach. Intertidal, exposed strand, mean high tide mark, depth in substratum 0.30 m; mean particle size 0.250 mm. So = 1.61. Gravel 0%, sand 99.95%, silt-clay 0.05%.
- Station 9: 34°41.36'N, 76°41.12'W; Bogue Banks, Fort Macon. Intertidal, exposed strand, mean high tide mark, depth in substratum 0.30 m; mean particle size 0.350 mm, So = 1.87. Gravel 0.50%, sand 99.43%, silt-clay 0.07%.
- Station 10: 34°40.40'N, 76°36.50'W; Schackleford Banks, facing Back Sound. Intertidal, semi-protected, mean high tide mark, depth in substratum, 0.30 m; mean particle size 0.450 mm, So = 1.19. Gravel 0%, sand 99.87%, silt-clay 0.13%.

Station 11: 34°40.25'N, 76°37.00'W; Schackleford Banks, facing open Ocean. Intertidal, exposed strand, mean high tide mark, depth in substratum 0.40 m; mean particle size 0.500 mm, So = 2.20. Gravel 0%, sand 99.99%, silt-clay 0.01%.

Station 12: 34°38.37'N, 76°30.52'W; Core Banks, lighthouse Bay, facing Core Sound. Intertidal, semi-protected, mean high tide mark, depth in substratum 0.20 m; mean particle size 0.340 mm, So = 1.25. Gravel 0%, sand 99.82%, silt-clay 0.08%.

Station 13: 34°38.28'N, 76°30.36'W; Core Banks, facing open Ocean. Intertidal, exposed strand, mean high tide mark, depth in substratum 0.40 m; mean particle size 0.450 mm. So = 2.14. Gravel 0%, sand 99.99%, silt-clay 0.01%.

Station 14: 34°11.07'N, 76°11.06'W; off the coast, continental shelf, depth 60 m. "Amphioxus sand."

Station 15: 34°10.06'N, 76°10.00'W; off the coast, continental shelf, depth 56 m. "Amphioxus sand."

SYSTEMATIC SECTION

Henlea Michaelsen, 1889

Henlea ventriculosa (Udekem, 1854)

Enchytracus ventriculosus Udekem, 1854, page 864, Figures 1, 4, 6-9.

Henlea ventriculosa (Udekem). Michaelsen, 1889, page 31; 1900, page 69; Ude, 1929, page 56; Bülow, 1955, page 254, plate 41, Figures 1-2; 1957, page 74; Nielsen and Christensen, 1959, page 62, figures 50, 53, 57; Cekanovskaya, 1962, page 300, Figure 189.

TYPE MATERIAL: Not designated, not located.

TYPE LOCALITY: Belgium.

DESCRIPTION: The species conforms to the original description as emended by Michaelsen (1889) and by Nielsen and Christensen (1959).

HABITAT: Salt marshes, above the upper part of the shore.

DISTRIBUTION: Cosmopolitan. Europe: Finland, Sweden, Denmark, Germany, Poland, U. S. S. R., Italy, Belgium, France, Great Britain, Eire. New Zealand. South America. New records for North America: Massachusetts; station 1, (4/3) North Carolina; station 1, (2/2) (refer to number of specimen and their maturity, for example, (4/3) and (2/2) mean: 4 specimens, 3 mature and 2 specimens, 2 mature).

Cernosvitoviella Nielsen and Christensen, 1959

Cernosvitoviella immota (Knöllner, 1935)

Enchytracoides immotus Knöllner, 1935b, page 438, Figures 9-13; Bülow, 1955, page 255, plate 41, Figures 5-6; 1957, page 85.

Cernostotoziella immota (Knöllner). Nielsen and Christensen, 1959, page 40. Figures 19–22.

TYPE MATERIAL: Not designated and not located.

TYPE LOCALITY: Kiel Bay, Western Germany.

DESCRIPTION: The species conforms to the original description, supplemented by Nielsen and Christensen (1959).

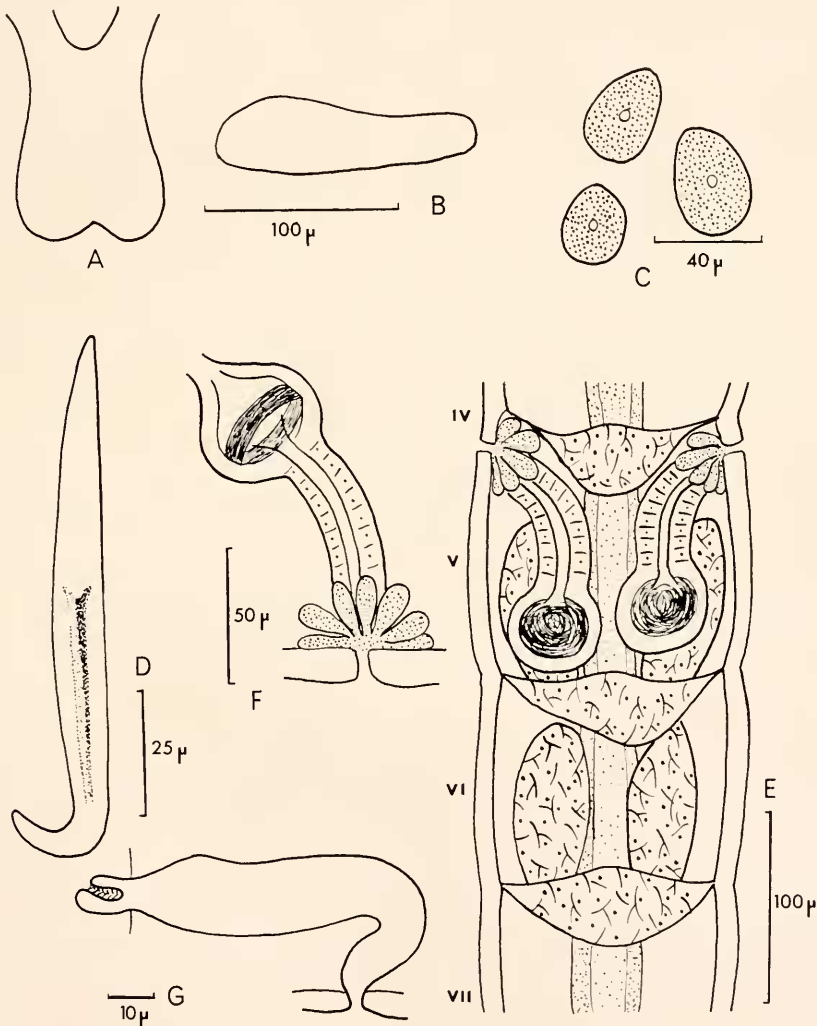


FIGURE 1. *Lumbricillus codensis* nov. sp. A, brain in dorsal view; B, brain in lateral view; C, coelomocytes; D, setae; E, dorsal view of septal glands and spermathecae (the ental ducts are not visible dorsally); F, spermatheca, detail; G, nephridium.

HABITAT: Salt marshes, above upper part of the shore.

DISTRIBUTION: Europe: widely distributed, Finland, Sweden, Denmark, Germany, British Isles, France. New records for North America: Massachusetts; station 1, (2/2).

Enchytracus Henle, 1837

Enchytracus albidus Henle, 1837

Enchytracus albidus Henle, 1837, page 74; Michaelsen, 1900, page 89; Knöllner, 1935b, page 449; Cernovitov, 1937, page 291; Bülow, 1957, page 91; Nielsen and Christensen, 1959; page 91, Figures 95–100; Cekanovskaya, 1962, page 307, Figure 193.

SYNONYMS: *Halodrilus littoralis* Verrill, 1873; *Enchytracus littoralis* (Verrill), Smith, 1895; *Enchytracus mobii* Michaelsen, 1886; *Enchytracus sabulosus* Southern 1906; *Litorca krumbachi* Cejka, 1913; *Enchytracus constrictus* Backlund, 1947.

TYPE MATERIAL: not designated and not located.

TYPE LOCALITY: Kiel Bay, West Germany.

DESCRIPTION: The species conforms to the reviewed description of Nielsen and Christensen (1959).

HABITAT: Salt marshes, decaying seaweed, compost heaps, sewage beds, effluents.

DISTRIBUTION: Cosmopolitan. Europe: Finland, Denmark, Sweden, British Isles, Holland, France, Greenland, South Patagonia, Uruguay, Tierra del Fuego. North America: New Haven, Woods Hole, Sea Isle City, New Jersey, Casco Bay, Maine (Verrill, 1873; Smith, 1895; Moore, 1905; Welch, 1917); Cold Spring Harbor, Long Island, New York (Hunt, 1915); Newport River, North Carolina (Wells, 1961). New records in North America: Massachusetts: station 1 (100/74); station 2, (63/52). North Carolina: station 1, (6/6); station 3, (3/3).

Enchytracus capitatus Bülow, 1957

Enchytracus capitatus Bülow, 1957, page 93, Figures 13–17; Nielsen and Christensen 1959, page 92; 1963a, page 14, Figure 11.

TYPE MATERIAL: Not designated, not located.

TYPE LOCALITY: West Germany, Kimbrischen Halbinsel, among *Armeria* on dike at Büsum.

DESCRIPTION: The species conforms entirely to the original description, reviewed by Nielsen and Christensen (1959, 1963a).

HABITAT: Driftline of seaweed deposit; intertidal sandy beaches in upper shore; meiobenthos.

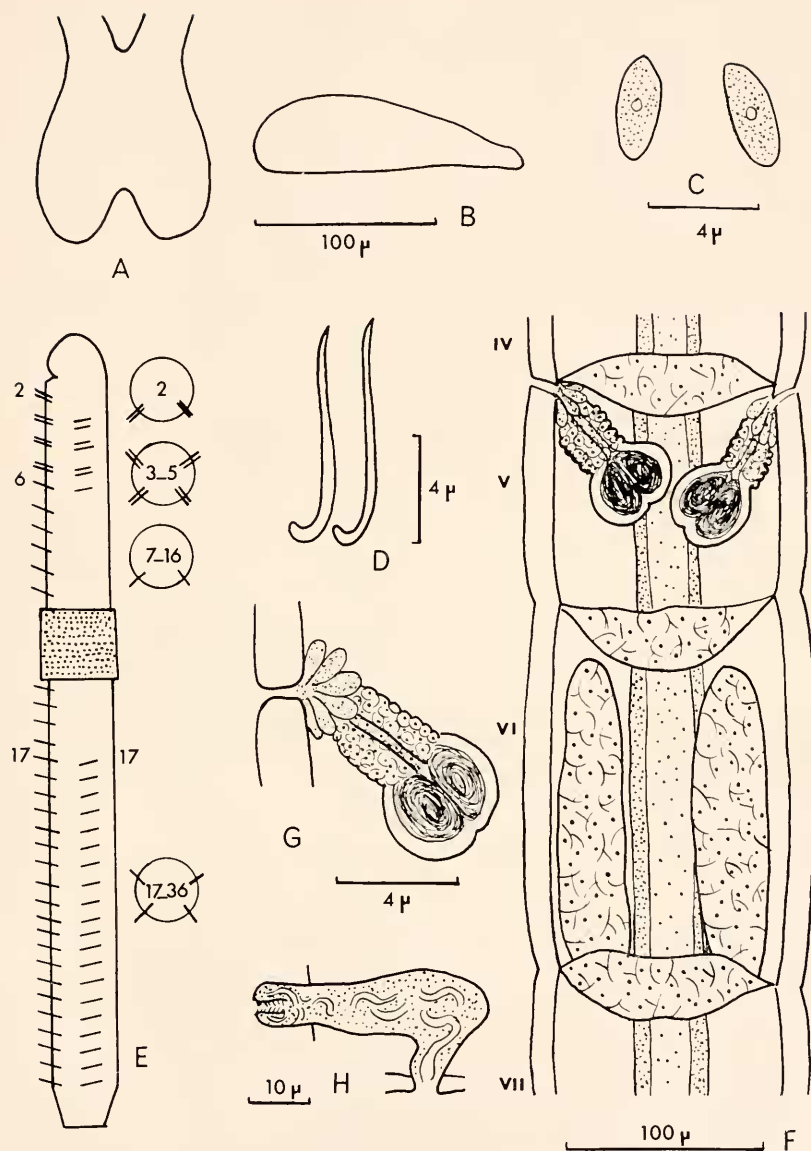


FIGURE 2. *Marionina zeelchi* nov. sp. A, brain in dorsal view; B, brain in lateral view; C, coelomocytes; D, setae; E, complement of setae in diagrammatic view; F, dorsal view of septal glands and spermathecae (the ental ducts are not visible dorsally); G, spermatheca, detail; H, nephridium.

DISTRIBUTION: Europe: Denmark, West Germany, France Atlantic and Mediterranean coasts. New records for North America. Massachusetts: station 1, (13/10); station 2 (122/100); station 3, (258/234); station 5, (36/26). North

Carolina: station 1, (6/5); station 2, (7/4); station 3 (21/17); station 5, (8/5); station 7, (5/1); station 10, (50/38).

Lumbricillus Ørsted, 1844

Lumbricillus lineatus (Müller, 1774)

Pachydrilus lineatus (Müller). Ude, 1929, page 60, Figure 76; Knöllner, 1935b, page 435; Bülow, 1955, page 254, plate 41, Figures 3-4.

Lumbricillus lineatus (Müller). Welch, 1917, page 123; Bülow, 1957, page 76; Nielsen and Christensen, 1959, page 100, Figures 109-112; Cekanovskaya, 1962, page 310, Figure 197.

Synonyms: *Lumbricillus verrucosus* (Claparède, 1864); *Lumbricillus clapedeanus* Ditlevsen, 1904; *Lumbricillus agilis* Moore, 1905

TYPE MATERIAL: not designated and not located.

TYPE LOCALITY: Denmark.

DESCRIPTION: The species conforms to the reviewed descriptions of Ude, 1929, and Nielsen and Christensen, 1959.

HABITAT: Salt marshes, in upper littoral zone; driftline seaweed deposit.

DISTRIBUTION: Europe: widely distributed. Helbrides, Tierra del Fuego. North America: Casco Bay, Maine to Vineyard Sound, Massachusetts (Moore, 1905, page 395); Woods Hole, Massachusetts (Welch, 1917, page 123). New records in North America: Massachusetts: station 2, (18/14); station 3, (15/9). Not found in North Carolina.

Lumbricillus codensis nov. sp.

Figure 1

HOLOTYPE: United States National Museum (U. S. N. M.), Cat. No. 43476. Cape Cod Bay, Massachusetts, U. S. A. 41°48.00'N, 70°31.20'W. Depth 6.7 meters.

PARATYPES: U. S. N. M. Cat. No. 43477. Five individuals as type locality; U. S. N. M. Cat. No. 43478, one individual from 41°53.00'N, 70°31.20'W, depth 12.2 meters, Gray Museum, Marine Biological Laboratory, Woods Hole, 2130, three individuals as type locality, 1930, one individual from 41°54.30'N, 70°08.00'W, depth 15.6 meters, 2130, one individual from 41°49.00'N, 70°31.20'W, depth 11.9 meters.

DERIVATION: "codensis" from Cape Cod Bay, Massachusetts, U. S. A.

DESCRIPTION: Small to medium sized, length 6-12 mm, diameter 140-160 μ . 45 to 58 segments. Color whitish. Dorsal setal bundles absent, ventral bundles present, each containing only one straight seta, strongly hooked proximally, thickest in the middle and with a longitudinal depression (Fig. 1, D). Cutaneous

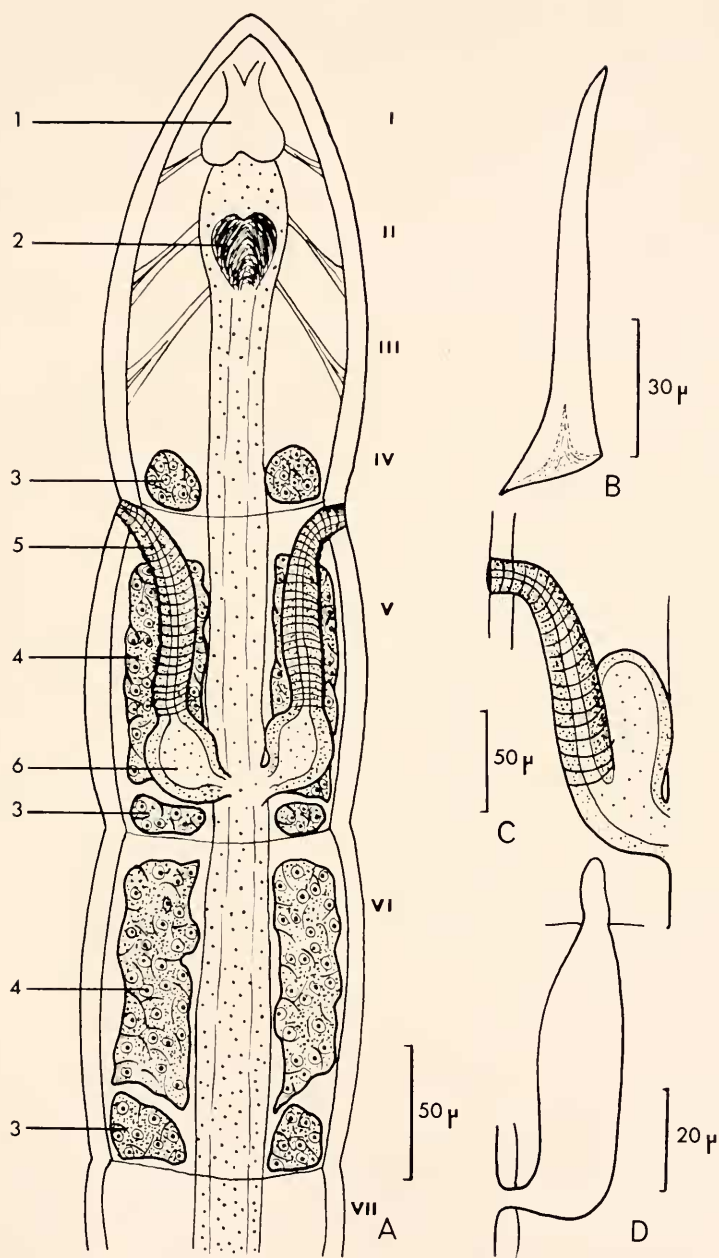


FIGURE 3. *Hemigrania postclitellochaeta* (Knöllner, 1935). A, dorsal view of septal glands and spermathecae: 1—brain, 2—pharynx, 3—primary septal glands, 4—secondary septal glands, 5—ectal canal of spermatheca, 6—ampulla of spermatheca, B, setae; C, spermatheca, detail; D, nephridium.

glands small and irregularly scattered. Brain longer than wide, posterior margin notched (Fig. 1, A-B). Three pairs of septal glands in IV/V-VI/VII, all united mid-dorsally, those in V/VI and VI/VII with ventral lobes, those in VI/VII large (Fig. 1, E). Chloragogen cells present from VI, particularly dense in postclitellar segments, they contain refractile globules. Coelomocytes oval or pear-shaped, $\frac{1}{3}$ to $\frac{1}{2}$ length of setae, with small granules. Dorsal vessel originates in XIII or XIV, blood colorless or faintly red. Nephridia with postseptale elongate, efferent duct arising terminally, anteseptale consisting of funnel only (Fig. 1, G). Irregularly lobed seminal vesicle, may occupy X and XI. Sperm funnel up to twelve times longer than wide, length approximately two times diameter of worm, collar regular and slightly narrower than funnel body. Sperm duct very long, irregularly coiled in XII or extending as far back as XX. Penial bulb compact, medium sized. Clitellum extends over XII- $\frac{1}{2}$ XIII, prominent gland cells arranged in transverse rows. Usually only one mature egg present at a time. Spermatheca with subspherical ampulla sharply defined from both ectal and ental ducts, ental duct short, communicating with oesophagus, ectal duct 2-3 times longer than wide, ectal orifice surrounded by a ring of 10-13 large club shaped glands, ectal duct 2-3 times longer than ampulla (Fig. 1, E, F).

HABITAT: Subtidal sands: Mean particle size between 0.336 mm and 0.795 mm.

DISTRIBUTION: Known only from Cape Cod Bay, Massachusetts, U. S. A.; material received from the Systematics-Ecology Program's Biotic Census, stations: 1412E1, (1/1); 1412E4, (24/22); 1530E3, (2/2); 1730E3, (46/38); 1812E1, (127/98); 1812E2, (286/204); 1812E4, (20/17); 1812E5, (72/58); 1930E3, (3/2); 2130E2, (78/64).

REMARKS: The shape and arrangement of the setae of *L. codensis* have no equivalent in other species of the genus. The single large and straight setae in each ventral bundle resemble those of species included in the genera *Hemigrania* nov. gen. and *Grania* Southern, 1913. However, on the morphological evidence of septal glands (no secondary glands, primary glands attached dorsally), peptonephridia (absent), nephridia (anteseptale consisting of funnel only) and spermatheca, it appears that the genus *Lumbricillus* Ørsted, 1844 is more appropriate for this species.

Marionina Michaelsen, 1889

Marionina southerni (Cernosvitov, 1937)

Pachydrilus Marionina southerni Cernosvitov, 1937, page 293, *Marionina southerni* (Cernosvitov, 1937), Nielsen and Christensen, 1959, page 112, Figures 135-137; Lasserre, 1971.

SYNONYMS: *Enchytraeus lobatus* Southern, 1909; *Enchytraeus nodosus* Stephenson, 1911; *Fridericia pseudoargentea* Knöllner, 1935.

TYPE MATERIAL: not designated and not located.

TYPE LOCALITY: Ireland.

DESCRIPTION: The species conforms to the reviewed description of Nielsen and Christensen (1959).

HABITAT: Driftline of seaweed deposit on the middle stretch of the beach.

DISTRIBUTION: Europe: Sweden, Denmark, Scotland, North Wales, Ireland, Germany, France (Atlantic and Mediterranean). New records for North America. Massachusetts: station 1, (2/2); station 2, (15/11); station 4, (7/4); station 5, (8/6). North Carolina: station 3, (12/9); station 4, (4/3); station 6, (13/10); station 10, (9/8).

Marionina spicula (Leuckart, 1847)

Enchytracus spiculus Leuckart, 1847, page 146; Ude, 1929, page 70, Figure 80; Bülow, 1957, page 92.

Marionina spicula (Leuckart), Nielsen and Christensen, 1959, page 115, Figures 145–148; 1963a, page 20; Lasserre, 1971.

TYPE MATERIAL: not designated and not located.

TYPE LOCALITY: Germany, Helgoland.

DESCRIPTION: The species conforms to the reviewed description of Nielsen and Christensen (1959).

HABITAT: Driftline of seaweed deposit, on the middle stretch of the beach; intertidal sandy beaches, upper to lower shore, meiobenthos.

DISTRIBUTION: Europe: widely distributed, Denmark, Germany, Belgium, Poland, France Atlantic and Mediterranean, Bulgaria Black Sea. New records for North America. Massachusetts: station 1, (122/87); station 2, (118/96); station 3, (111/82); station 4, (151/101); station 5, (186/113); station 6, (102/88). North Carolina: station 1, (18/12); station 4, (22/11); station 6, (9/8); station 7, (32/27); station 8, (15/10); station 9, (13/9); station 10, (400/268); station 11, (12/8); station 12, (54/48).

Marionina subterranca (Knöllner 1935)

Michaelsena subterranca Knöllner 1935a, page 136, 1935b, page 455, Figures 26–28; Bülow, 1957 page 94; Nielsen and Christensen, 1959, page 110, Figures 132–134; 1963a, page 19; Lasserre, 1966, page 315, 1971.

SYNONYMS: *Michaelsena* n. sp. Bülow 1957; *Hichaelsena glandulifera* Jansson, 1961.

TYPE MATERIAL: not designated and not located.

TYPE HABITAT: Kiel Bay, West Germany.

DESCRIPTION: The species conforms to the original description reviewed by Nielsen and Christensen (1959, 1963a).

HABITAT: Intertidal sandy beaches, on lower part of the beach, at ground water level, meiobenthos.

DISTRIBUTION: Europe: widely distributed, Denmark, Sweden, Finland, Germany, British Isles, France (Atlantic and Mediterranean), Bulgaria (Black sea). North Africa: Tunisia, Algeria. New records for North America. Massachusetts: station 1, (8/5); station 2, (181/139); station 3, (603/394); station 4, (242/101); station 5, (986/421); station 6 (308/116). North Carolina: station 2 (7/6); station 5, (6/4); station 6, (5/3); station 7, (2/2); station 8, (13/11); station 9, (22/15), station 10, (42/29), station 11, (7/2); station 12, (31/22); station 13, (8/5).

Marionina achaeta Lasserre, 1964

Michaelsena sp. Hagen, 1951, cited in Bülow 1957, page 95; Nielsen and Christensen, 1959, page 110.

Marionina achaeta Lasserre, 1964, page 87; 1966, page 300, Figure 1; Tynen and Nurminen, 1969, page 151, Lasserre 1971.

TYPE MATERIAL: Museum National d'Histoire Naturelle, Paris, Cat. No. A.777-AA 44.

TYPE LOCALITY: Bassin d'Arcachon, Atlantic, France.

DESCRIPTION: The species conforms to the original description (Lasserre 1964, 1966). This species was discovered by Hagen (1951) in Germany, named by him *Michaelsena achaeta* n. sp., but the description was not published. The identity of the German and French material was checked by Lasserre (1964) who retained the proposed name by Hagen and gave the description.

HABITAT: Intertidal sandy beaches, in upper shore and at ground water level on lower shore, meiobenthos.

DISTRIBUTION: Europe: widely distributed, Sweden, Denmark, Germany, France (Atlantic and Mediterranean), Bulgaria (Black Sea). North Africa: Tunisia, Algeria. New records for North America. Massachusetts: station 2, (3/1) station 3, (28/16); station 5 (41/12); station 6 (34/18). North Carolina: station 1, (11/5); station 2, (5/3); station 3, (33/21); station 4 (17/11); station 6, (19/7); station 7, (4/1); station 8, (7/2); station 10, (12/5); station 11, 1 immature; station 12, (8/3).

Marionina preclitellochacta Nielsen and Christensen, 1963

Marionina sp. Jansson, 1962.

Marionina preclitellochacta Nielsen and Christensen, 1963b, page 12, Figures 18-19; Lasserre, 1966, page 314; 1967a, and b; Tynen and Nurminen, 1969, page 151; Lasserre, 1971.

TYPE MATERIAL: Møls Laboratory, Femmøller, Denmark.

TYPE LOCALITY: Sweden, Swedish west coast.

DESCRIPTION: The species conforms with the original description (Nielsen and Christensen, 1963b). This species was discovered by Jansson (1962) in Sweden and named by him *Marionina preclitellochaeta* n. sp. Jansson deferred the description to a later publication. Nielsen and Christensen (1936) found the species in Denmark, the identity of the Swedish and Danish material was checked by Nielsen and Christensen who retained the proposed name and gave the description.

HABITAT: Intertidal sandy beaches, middle to lower shore, at ground water level.

DISTRIBUTION: Europe: Sweden, Denmark, France Atlantic. New records for North America. Massachusetts: station 1, (170/130); station 2 (218/159); station 3, (106/67); station 5, (319/202); station 6, (216/109). North Carolina: station 4, (83/71); station 8, (9/4).

Marionina welchi nov. sp.

Figure 2

HOLOTYPE: U. S. N. M. Cat. No. 43479, Cape Cod Bay, Massachusetts, U. S. A., 41°54.00'N, 70°08.40'W, depth 17.0 meters.

PARATYPES: U. S. N. M. Cat. No. 43480, three individuals as type locality; U. S. N. M. Cat. No. 43481, one individual from 41°45.30'N, 70°16.00'W, depth 14.6 meters; Gray Museum at the Marine Biological Laboratory, Woods Hole, Massachusetts, 1412, one individual as type locality.

DERIVATION: "*welchi*" = in honor of P. S. Welch, long an outstanding American authority on the Enchytraeidae.

DESCRIPTION: Small to medium-sized, length 5–10 mm, diameter 100–150 μ . 30–44 segments. Color white. Straight setae with proximal hook (Fig. 2, D), dorsal setal bundles absent in segment II and VII–XVI, two dorsal setae per bundle in segment III–V, one in segment VI, and one per bundle from segment XVII; ventral bundles containing two setae in segments II–V and one from segment VI (Fig. 2, E). Cutaneous glands arranged in five to seven transverse rows on each segment. Brain longer than wide, posterior end incised (Fig. 2, A–B). Three pairs of septal glands in IV/V–VI/VII, all united middorsally, those in VI/VII with large ventral lobes (Fig. 2, F). Chloragogen cells present from V and forming a dense layer from VI, contain refractile globules. Coelomocytes spindle-shaped, $\frac{1}{2}$ length of setae, with small granules (Fig. 2, C). Dorsal vessel originates in XIV, blood colorless. Anteseptale of nephridium ovoid, with coils of nephridial canal, postseptale elongate (Fig. 2, H). Seminal vesicle compact in segment XI. Sperm funnel $2\frac{1}{2}$ times longer than wide, length approximately half diameter of the worm, collar regular and about half as wide as funnel body. Sperm duct narrow, of medium length and irregularly coiled in XII. Penial bulb large and compact. Clitellum extends over XII– $\frac{1}{2}$ XIII, gland cells arranged in transverse rows. Only one mature egg present at a time. Spermatheca with

ectal duct short and covered by fused glands closely packed, rosette of six to eight separate glands at the ectal orifice, ampulla subspherical, length approximately equal to that of ectal and connected dorsally with oesophagus through a short ental duct (Fig. 2 F-G).

HABITAT: Subtidal sands: Mean particle size between 0.466 mm and 0.795 mm.

DISTRIBUTION: Known only from Cape Cod Bay, Massachusetts, U. S. A.; material received from the Systematics-Ecology Program's Biotic Census; stations: 1412E4, (11/7); 2028E5, (4/3); 2318E1, (2/2), 2318E4, (1/1).

REMARKS: *M. welchi* is related to *M. subtilis* (Ude, 1896), *M. paucispina* (Eisen, 1904) and *M. normani* (Michaelsen, 1907) described, respectively, from Tierra del Fuego, Santa Barbara, California and Western Australia. These species form a complex of Enchytraeidae characterized by reduction in the number of dorsal and ventral setae and by the shape of the spermatheca. The original description of *M. normani* was based on immature individuals and it must be considered a species dubium.

Hemigrania nov. gen.

DEFINITION: Peptonephridia absent. Three pairs of primary septal glands in segments IV, V, VI not united dorsally, secondary glands always present. Setae large and straight, very broad at the inner end, without nodulus; only one seta per bundle. Anteseptale of nephridia consists of funnel only. Spermatheca attached dorsally to the oesophagus, ectal duct and orifice without glands or diverticulae.

TYPE SPECIES: *Hemigrania postclitellochaeta* (Knöller, 1935b) nov. comb.

Figure 3

REMARKS: The species here referred to the new genus *Hemigrania* belonged in the genus *Michaelsena* Ude, however Nielsen and Christensen (1959) recognized *Michaelsena* as being a wholly artificial genus and transferred the species *postclitellochaeta* to *Marionina* Michaelsen, 1889. Recently, Lasserre (1967a, 1967b) was able to examine living and fixed specimens of the species *postclitellochaeta* and recognized that it differed in many ways from the other species of *Marionina*. The genus *Grania* Southern, 1913 was obviously a more suitable recipient, nevertheless, the author concluded that it might become necessary to remove it to a separate genus (Lasserre, 1967a, 1967b). This course has been followed in the present work. It is evident from a study of French and North American material, that the species described by Knöllner (*postclitellochaeta*) differed consistently from species of *Grania* Southern, and from species of other genera mainly by the presence of secondary glands and absence of peptonephridia and the shape of spermatheca. These differences are of sufficient importance to transfer *postclitellochaeta* to a new genus. The same conclusion is drawn for two species described by Michaelsen (1888 and 1907) from South Georgia and South West Australia: *Enchytraeus monochaetus* Michaelsen, 1888 and *Michaelsena principissae* Michaelsen, 1907. The important character differentiating the genus *Grania* Southern, 1913, and *Hemigrania* nov. gen. is the presence or absence of pepto-

nephridia. *Hemigrania* nov. gen. is, evidently, closely related to the genera *Grania* and *Marionina* but differs in two characteristic features, i.e., absence of peptonephridia and presence of secondary septal glands. The list of characters given in the definition of *Hemigrania* nov. gen. also enables it to be distinguished from other genera of Enchytraeidae.

Hemigrania postclitellochaeta (Knöllner, 1935) nov. comb.

Michaelsena postclitellochaeta Knöllner, 1935b, page 449, Figures 19–25; Bülow, 1957, page 95.

Marionina postclitellochaeta (Knöllner), Nielsen and Christensen, 1959, page 110.

Grania postclitellochaeta (Knöllner), Lasserre 1966, pages 299, 312–314; 1967b, page 279, page 280.

TYPE MATERIAL: not designated and not located.

TYPE LOCALITY: Kiel Bay, West Germany, off the coast.

OTHER MATERIAL: Museum National d'Histoire Naturelle, Paris, Cat. No. A.777-AA 48 Gulf of Gascogne, France. U. S. N. M., Cat. No. 43482, Cape Cod Bay, Massachusetts, U. S. A., three individuals from 41°54.00'N, 70°08.40'W, depth 17.1 meters; Gray Museum, Marine Biological Laboratory, Woods Hole, Massachusetts, Sep 1910/1930, two individuals from 41°49.30'N, 70°05.30'W, depth 6.9 meters, and from 41°50.00'N, 70°31.20'W, depth 10.4 meters.

DESCRIPTION: (from literature and author's observations). Small to medium-sized, length 5–10 mm, diameter 100–130 μ , 32–51 segments. Color whitish. Dorsal setal bundles absent, ventral setae one per bundle, absent from anterior segments 1 to XIV or XVII, setae large, straight and very broad proximally (Fig. 3, B). Cutaneous glands small and irregularly scattered. Brain about as long as broad, posterior end incised (Fig. 3 A1). Septal glands not united dorsally, three pairs of primary glands present in IV, V, VI with arrangement of secondary glands variable: usually one pair of primary glands in IV, one pair of primaries and one pair of secondaries in V and VI (Figs. 3 and 4). Chloragogen cells present from VII, with refractile globules. Coelomocytes oval abundant posteriorly, $\frac{1}{3}$ length of setae, with refractile granules. Dorsal vessel originated behind clitellum in XX, blood faintly yellow. Nephridia with postseptale elongate, efferent duct arising terminally, anteseptale consisting of funnel only (Fig. 3, D). Compact seminal vesicle present. Sperm funnel four times longer than wide, length approximately same as diameter of the worm, collar regular, nearly as wide as funnel itself. Sperm duct long, extending as far back as XVI. Penial bulb compact and large. Clitellum extends over XII– $\frac{1}{2}$ XIII, gland cells arranged in transverse rows. One mature egg present at a time. Spermatheca with ectal duct long cylindrical and muscular, devoid of glands along its length and aperture, opening dorso-laterally, ampulla globular and connected dorsally with esophagus (Fig. 3A, 5–6; C).

HABITAT: Subtidal coarse sands "Amphioxus sand."

DISTRIBUTION: Europe: Baltic Sea, Kiel Bay, Germany, France (Atlantic and Mediterranean). New records for North America: Cape Cod Bay, Massachusetts;

material received from the Systematics-Ecology Program's Biotic Census; stations: 0612-E1, (1/1); 1412-E4 (23/19); 1812-E2, (209/177); 1910-E1, (2/2); 1930-E2, (1/1); 2008-E5, (4/4). Continental shelf off the coast of North Carolina; station 14 and 15 (3/3).

NOTES ON GEOGRAPHICAL DISTRIBUTION AND HABITAT

The marine Enchytraeidae, in common with Tubificidae and Naididae, are widely distributed and abundant oligochaetes. They live in littoral and subtidal habitats. In Europe many species occur in the Atlantic Ocean, Baltic Sea, the Mediterranean and Black Seas. The Enchytraeidae of other continents have not

TABLE I

*Enumeration of meiobenthic Enchytraeidae collected from exposed and semi-protected beaches in Massachusetts and North Carolina (Spring 1969).
Number of beaches examined is in parentheses*

Species	Average numbers of animals per 500 cc of sediment			
	Massachusetts		North Carolina	
	Exposed beaches	Semi-protected beaches	Exposed beaches	Semi-protected beaches
<i>E. capitatus</i>	13 (1)	139 (3)	5 (1)	26 (3)
<i>M. southerni</i>	2 (1)	10 (3)	13 (1)	8 (3)
<i>M. spicula</i>	122 (1)	173 (5)	18 (5)	158 (3)
<i>M. subterranea</i>	8 (1)	464 (5)	9 (6)	26 (3)
<i>M. achaeta</i>	3 (1)	34 (3)	8 (4)	23 (4)
<i>M. preclitellochaeta</i>	170 (1)	215 (4)	9 (1)	83 (1)
Total genera	2	2	2	2
Total species	6	6	6	6
Total individuals/500 cc	436	1035	62	324

been studied to the same extent; the fact that species have not been reported from outside European countries certainly does not indicate that their distributions are restricted to Europe.

Eleven species, described from Europe, widely distributed on this continent, were hitherto unknown from the eastern coast of North America. Two species are apparently limited to Cape Cod Bay, Massachusetts: *Lumbricillus codensis* nov. sp. and *Marionina welchi* nov. sp. The specimens of cosmopolitan species collected by the author in Europe and eastern North America (Massachusetts and North Carolina) are morphologically inseparable.

Both littoral and sublittoral biotopes are inhabited by Enchytraeidae. Four categories of habitats were investigated.

(a) Salt marshes, situated above the upper part of the shore in the supralittoral area where low salinities occur. The dominant species are *Hecile ventriculosa*, *Cernosvitoviella immota* and *Enchytraeus albidus*.

(b) Gently sloping beaches where decayed seaweeds are scattered in and on the sand or on the gravelly sediment between the high and low tide marks. Four abundant species live in this habitat; *Enchytracus capitatus*, *Lumbricillus lineatus*, *Marionina spicula* and *Marionina southerni*.

(c) Intertidal sand beaches which possess meiobenthic communities of oligochaetes have a well-sorted sediment and a very small amount of detritus. The species diversity and geographical distribution of these communities are fairly well known for the Western and North-western coasts of Europe (Lasserre, 1971). The density for each species, in any 500 cc sample, collected during the study, is given in the Systematic Section. Examples are given in Table I for beaches in Massachusetts and North Carolina. Maximum densities are found in semi-protected beaches; 1035 individuals per 500 cc in Massachusetts, 324 individuals per 500 cc in North Carolina. The exposed strands have only 436 individuals per 500 cc in Massachusetts and 62 individuals in North Carolina. It seems that Enchytraeidae are not so abundant in North Carolina as in Massachusetts, but it will be necessary to compare the populations over their whole life span. Three species, *Enchytracus capitatus*, *Marionina preclitellochaeta* and *Marionina achaeta* were found in the upper shore; *Marionina subterranea*, as well as *Marionina preclitellochaeta* and *Marionina achaeta*, were collected from the middle to the lower shore, where low salinities may occur, together with the tubificid *Phallodrilus monospermathecus* (Knöllner). In the case of both the middle and upper shore populations, the maximum densities were found at depths between 5 and 60 cm from the surface. All these observations are in agree with the studies of Jansson (1966, 1968) and Lasserre (1967a, 1970) on beaches in Sweden and France. All species have a broad range of grain size tolerance. The optimum mean grain size between 0.250 mm and 0.900 mm in Massachusetts and between 0.250 mm and 0.500 mm in North Carolina, with a maximum value of 0.20% of fine particles smaller than 0.063 mm. The sorting coefficient, ranging from 1.25 to 2.20 is close to that of Trask's definition of a well-sorted sediment.

(d) Few, but interesting, Enchytraeidae live in subtidal sediments composed mainly of coarse sands. During the Biotic Census of Cape Cod Bay, in 1968, approximately 100 (of a total of 700) subtidal samples were examined for oligochaetes, only 18 contained Enchytraeidae and seven of these samples, consisting of coarse sediment, contained the species *Hemigrania postclitellochaeta*, which is also present in the "Amphioxus sand" (off Cape Hatteras, North Carolina) and widely distributed in coarse subtidal sediments in Europe (Lasserre 1966, 1967a, b). *Lumbricillus codensis* nov. sp. and *Marionina welchi* nov. sp. live in subtidal sediments of Cape Cod Bay composed of 61.8% to 99.9% of sand, at depth between 2 meters and 19 meters. The optimum mean grain sizes are between 0.466 mm and 0.795 mm with a maximum value of 1.86% of fine particles smaller than 0.063 mm. The sorting coefficient ranging from 0.50 to 0.68 is close to that of Trask's definition of a very well-sorted sediment.

DISCUSSION

The abundance of marine Enchytraeidae in North America is indicated by the fact that in spite of the small number of investigations which have been made in the family, six genera, *Henlea* Michaelsen, *Cernosvitoviella* Nielsen and Christ-

ensen, *Enchytracus* Henle, *Lumbricillus* Ørsted, *Marionina* Michaelsen, *Hemigrania* nov. gen. have been shown to be present on this continent. It seems reasonable to predict that future investigations will reveal many other genera and species. The marine enchytraeidae fauna of the Carolinian province is composed of eurythermic species which are very abundant on the north eastern coast of North America and widely distributed in western and north-western Europe.

Field observations and preliminary experiments showed that American representatives of cosmopolitan species of *Marionina* exhibit great ability to withstand wide fluctuations of temperature and salinity, with minimum ranges of more than 25° C and 15‰. The homeostatic capabilities of the two cosmopolitan species *Marionina spicula* and *Marionina achacta*, collected in the Bay of Arcachon, France, were investigated experimentally (Lasserre 1969, 1970a, b, 1971). It was found that the overall consumption of oxygen in both species was statistically constant over a range of temperature and salinities spanning those normally encountered. There is some evidence to suggest that cosmopolitan marine Enchytraeidae have a world wide distribution reflecting their wide tolerance of physical factors.

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SUMMARY

1. Marine Enchytraeidae from the Eastern coast of North America were examined. Six genera and thirteen species are reported, four genera and eleven species are new to the American continent.

2. One new genus and two new species are described on material received from the Biotic Census of the Systematics-Ecology Program at the Marine Biological Laboratory: *Hemigrania* nov. gen., *Lumbricillus codensis* nov. sp. and *Marionina welchi* nov. sp. Three species are included in the new genus: *Hemigrania postclitellochacta* (Knöllner, 1934), *Hemigrania monochacta* (Michaelsen, 1888), *Hemigrania principissac* (Michaelsen, 1907); three species are related to *Marionina welchi* nov. sp.: *Marionina subtilis* (Ude, 1896), *Marionina paucispina* (Eisen, 1904) and *Marionina normani* (Michaelsen, 1907).

3. Marine Enchytraeidae are found in both littoral and sublittoral biotopes. Four categories of habitats are briefly described, (a) salt marshes, (b) the dirflint of seaweed deposit, (c) intertidal sand beaches, with well-sorted sediment and very small amounts of detritus, (d) the subtidal biotopes with very well-sorted sandy sediments.

4. The marine Enchytraeid fauna is composed of eurythermic cold water species, very abundant on the north eastern coast of North America (the Woods Hole region, Massachusetts), and also present under the warmer latitudes of the Beaufort region, North Carolina.

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